

Mortality and survival of semi-domesticated reindeer (*Rangifer tarandus tarandus* L.) calves in northern Finland

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Abstract: During the period 1999 to 2004 the reindeer calf survival and mortality were studied in two reindeer-herding cooperatives and in five herding-groups in northern Finland, where in total 1725 calves were fitted with mortality indicating radio-transmitters fixed on expandable neck collars. The calves were weighed and marked at the age of 2-5 days in calving corrals and also during earmarking in June/July, when the age of calves was 2-8 weeks. The rate, timing and causes of mortality of calves were investigated. In 1999-2001 in Ivalo reindeer-herding cooperative 4.6% of radio-collared calves and in 2002-04 in Käsivarsi reindeer cooperative 5.2% was found dead. The average mortality of the calves radio-collared during calving time in May, and monitored to the end of October, was 6.7% in Ivalo and 9.0% in Käsivarsi. From July on, the average mortality rates varied between 1.8-5.7% among reindeer herding-groups. On average 54 and 42% of all radio-collared calves found dead in Ivalo and Käsivarsi cooperatives were attributed to predation, and golden eagle was the most significant cause of death in both cooperatives killing 0-3.5% of radio-collared calves in different study areas and years. Golden eagle predation accounted for 33-43% of all radio-collared calves found dead, 55-59% of the cases with identified cause of death and 80% of all identified predation. Most of the calves killed by golden eagle were found during July and August mainly in the open areas, as in highlands, bogs and clear-cut forest areas. The mean body weight of the calves radio-collared in May (weights adjusted on June 1st) and found dead during the summer was significantly ($P<0.01$) lighter than the mean weight of survivors both in Ivalo and Käsivarsi. Furthermore, the midsummer body weights of the calves (weights adjusted on July 1st) killed by all predators and by golden eagles were significantly ($P<0.001$) lower than the mean weight of surviving calves in both cooperatives. However, the weights did not differ between depredated calves and those calves that succumbed due to other causes than predation. The results of this study emphasize the relative importance of golden eagle as a mortality factor for reindeer calves in the northern part of the Finnish reindeer husbandry area.

Key words: Semi-domesticated reindeer; *Rangifer*; calf mortality; predation; golden eagle; survival; radio telemetry.

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Introduction

Knowledge of juvenile survival and the influences of many intrinsic and environmental factors on mortality and survival rates are essential to improved understanding and modelling of dynamics of free-ranging populations. Many studies with northern deer species have demonstrated that low birth-mass, depressed condition, inability to nurse, and maternal re-

jection may predispose to early mortality (see Langenau & Lerg, 1976; Bergerud, 1980; Sams *et al.*, 1996; Tveraa *et al.*, 2003; Carstensen Powell & DelGiudice, 2005). During the life cycle the risk of death is usually greatest during the first year of life. It has been also suggested that the probability that a predator kills an individual is dependent on the prey's nutritional status (DelGiudice *et al.*, 2006).

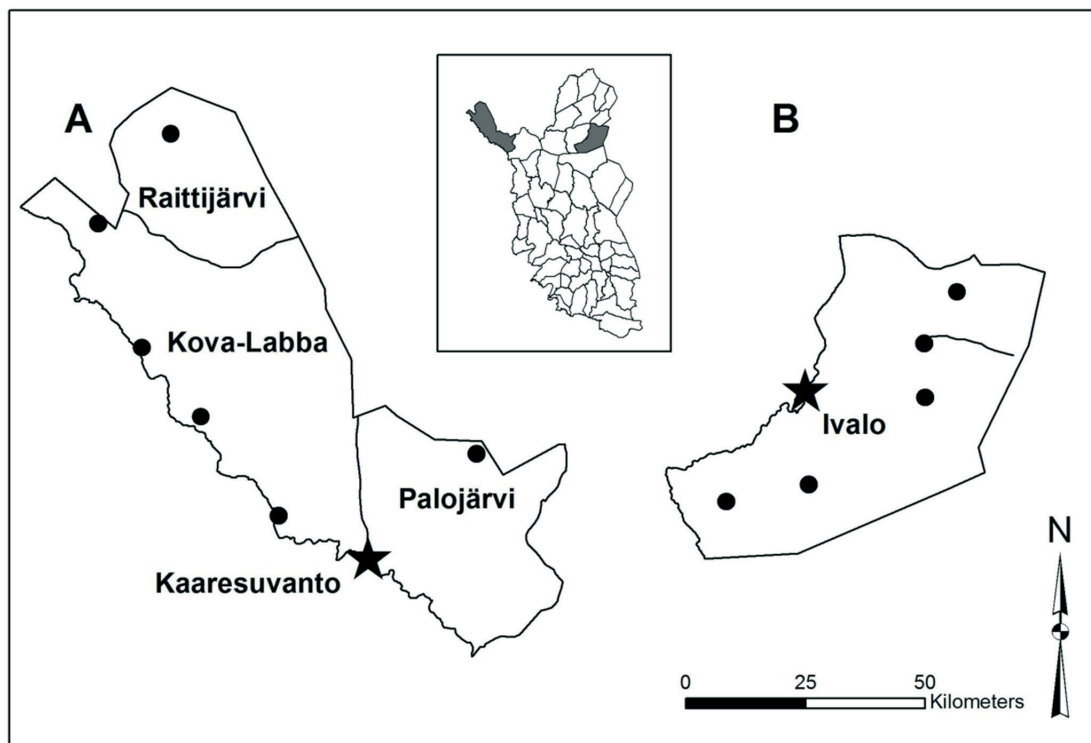


Fig. 1. Study areas within the Finnish reindeer husbandry area. The reindeer-herding cooperative of Ivalo (B) is divided into two herding-groups (Nellim and southern area of Ivalo) and Käsivarsi (A) into three herding-groups (Palojärvi, Kova-Labba and Raittijärvi). Reindeer calves were fitted with radio-collars in different corrals (●) in 1999–2004. The villages of Ivalo and Kaaresuvanto are marked on the map (★).

Many studies have shown the major role of large terrestrial carnivores on the neonate mortality of large and medium-sized ungulates (see Linnell *et al.*, 1995). Calf mortality is also an important factor in the population dynamics of many reindeer and caribou herds, and predation is suspected as the primary cause of mortality (Miller & Broughton, 1974; Page, 1985; Mahoney *et al.*, 1990; Skogland, 1991; Whitten *et al.*, 1992; Adams *et al.*, 1995; Valkenburg *et al.*, 2004; Norberg *et al.*, 2005, 2006; Nieminen, 2010). Caribou herds exposed to predation may lose even 50% of the annual calf crop prior to six months of age (Bergerud, 1980). Boertje (1984) suggested also that early predation of calves, independent of nutritional condition, was the key factor limiting the population in the Denali caribou herd in Alaska.

In the northern parts of Fennoscandia semi-domesticated reindeer *Rangifer tarandus tarandus* L. comprises an important source of prey for many predators. Apart of many herding activities and increasing supplementary feeding during winter months, reindeer are free-ranging most of the year also in Finland, especially during the summer, and share parts of their range with different predators including wolverine *Gulo gulo*, Eurasian lynx *Lynx lynx*, brown bear *Ursus arctos*, wolf *Canis lupus* and golden eagle *Aquila chrysaetos*. It is also well accepted that large carnivores may cause substantial losses in semi-domesticated reindeer by preying both adults and juveniles (Björvall *et al.*, 1990; Nybakk *et al.*, 2002; Danell *et al.*, 2006; Nieminen, 2009, 2010). Furthermore, also golden eagle and red fox *Vulpes vulpes*

have been shown to prey upon reindeer calves (Nybakk *et al.*, 1999; Tveraa *et al.*, 2003; Norberg *et al.*, 2006). The role of golden eagle as predator of reindeer calves is, however, not so well known as that of large carnivores. Only few studies (see Whitten *et al.*, 1992; Kvam *et al.*, 1998; Nybakk *et al.*, 1999; Valkenburg *et al.*, 2004; Norberg *et al.*, 2006) have shown predation by golden eagle to comprise a substantial part of the total first summer mortality in studied populations.

The aim of this study was to investigate the survival and the extent, timing and causes of reindeer calf mortality in two reindeer-herding cooperatives, Ivalo and Käsivarsi, both situated in northern Finnish Lapland. We hypothesized that 1) mortality peaks at the first summer months, 2) golden eagle predation on semi-domestic reindeer calves is remarkable in these cooperatives, 3) it occurs usually in more open habitats and higher elevations compared to other mortality (see Norberg & Nieminen, 2008), and 4) smaller than average calves are in greater risk to succumb and get preyed by golden eagles. This study is based partly on our earlier reports in Finnish (see Maijala *et al.*, 2002; Norberg & Nieminen, 2004; Norberg *et al.*, 2005).

Study areas

The reindeer-herding cooperative of Ivalo (ca. 130 reindeer owners), situated in the municipality of Inari, northern Finland (Ivalo village, 68°39'N, 27°33'E) covers a total land area of 2626 km². In Ivalo cooperative, there are two partly by a fence separated herding-groups: 1) Nellim and 2) Southern area (see Fig. 1). The reindeer-herding cooperative of Käsivarsi (ca. 160 reindeer owners), situated in the municipality of Enontekiö (Kaaresuvanto village, 68°27'N, 22°29'E), covers a total land area 4658 km², and it is the second largest among the 56 cooperatives in Finland. The cooperative of Käsivarsi is divided by fences into three

separate herding-groups: 1) Palojärvi, 2) Kovalabba and 3) Raittijärvi (Fig. 1). Both of the study cooperatives are situated in the north boreal vegetation zone (Ahti *et al.*, 1964). In Ivalo cooperative terrain is dominated by rolling hills with different aged forest stands of mainly Scots pine *Pinus sylvestris*. Mountain birch *Betula pubescens czerepanowii* grows in the slopes of the highest hills and only the tops of the highest fells are barren. In Käsivarsi, the area of coniferous forests is relative small and locates in the southern part of the cooperative. The mountains dominate the landscape, and the elevation ranges between 275 and 1320 m above sea level. During this study the mean snow depth in April was 56-99 cm in Ivalo and 59-68 cm in Käsivarsi. The mean temperature in July was 13.6-14.3 °C in Ivalo and 13.5-15.7 °C in Käsivarsi cooperative, respectively (Finnish Meteorological Institute).

There were on average 5660 reindeer (adults and calves after slaughtering) in the reindeer-herding cooperative of Ivalo during the study in 1999-2001, and 10 690 reindeer in Käsivarsi during 2002-04. The maximal reindeer number can be in Ivalo 6000 and in Käsivarsi 10 000. Reindeer densities (winter stock/km² land area) were almost equal, 2.1 in Ivalo and 2.3 in Käsivarsi. During 2000-03 in the whole northern reindeer husbandry area (including in total 13 cooperatives) the minimum numbers of large carnivores were: 45-50 brown bears, 40-45 wolverines, 5-10 lynx and 3 wolves (Kojola & Määttä, 2004). The most abundant among large carnivores was brown bear in Ivalo and wolverine in Käsivarsi cooperatives. However, the exact number of these elusive species within the study areas is not known. 90% of the known 400 golden eagle territories in Finland were situated in the reindeer husbandry area and the estimate for individual eagles before fall migration was around 1000 (Ollila, 2003). Most territories in Ivalo and Käsivarsi were situated in the alpine highlands, and about 16

golden eagles were living during this study in Ivalo and 21 in Käsivarsi reindeer-herding cooperatives (Ollila, pers. comm.).

Material and methods

In total 1725 reindeer calves (806 in Ivalo and 919 in Käsivarsi cooperatives, annually ca. 3% of all calves in the study areas) were fitted with mortality indicating radio-transmitters (Televilt Inc., Lindesberg, Sweden; frequency 230 MHz) fixed on expandable neck collars in different study areas during 1999-2004. Radio-collars weighed about 100 grams and corresponded 0.3-2.5% of the body weight of the calves at marking. Calf survival and cause-specific mortality were studied two years in the herding-groups of Nellim (1999-2000) and Raittijärvi (2002-03), and three years in other herding-groups (Southern area of Ivalo 1999-2001, Palojärvi and Kova-Labba 2002-04). 11 calves from Nellim herd were radio-collared at midsummer earmarking in 2001, and survival of these calves was included in the survival estimates of Nellim herd and Ivalo cooperative.

Calves were weighed and marked at the age of 2-5 days in calving corrals in May/June. In the corrals the females were fed for 1.5 month with silage and concentrates during spring and calving period. Midsummer earmarking took place in the last weeks of June and the first weeks of July, when the age of calves was 2-8 weeks. Calves were marked in five different corrals in Ivalo and six in Käsivarsi reindeer-herding cooperatives (see Fig. 1). Calves were sexed (950 females, 831 males and 17 sex not known) and weighed, and pelt colour was recorded. After securing that the radio-collared calves were reunited with their mothers, reindeer were released to the summer pastures.

After marking, signals of mortality transmitters, which activate after being 2.5 hours motionless, were radio-tracked both from the air (fixed-wing aircraft and helicopter) and by ground triangulation to locate dead calves.

Tracking was performed in 2-3 day intervals during summer until the end of August, and once per week in September and October. On the field, activated radio-collars were located by using hand receivers (Televilt RX-8910®, Televilt Inc., Lindesberg, Sweden and Tracker Maxima® and hound radars, Tracker Inc., Oulunsalo, Finland). Field observations of the site and carcass were recorded and photographed. Cause of death was first investigated in the field (e.g. evidence supporting presence of predator/scavenger species, such as tracks, scats and feathers/downs) and then supported by necropsies conducted by biologists in the laboratory of the Reindeer Research Station at Kaamanen. The presence of haemorrhages and perforations, both in the skin and soft tissues of the dead calf, were critical for determining the cause of death when depredation was suspected. If the combined evidence from the field site and the necropsy was inadequate, usually due to late discovery of carcass, the cause of death was classified as unknown (see also Bjärvall *et al.*, 1990; Norberg *et al.*, 2005, 2006).

Statistical analysis

Due to the difference in the marking time and age of calves the weight of the calves at marking ranged between 4.2-32 kg, and therefore for statistical analysis the weights were adjusted to 1st of June and to 1st of July by using a daily growth rate of 270 grams (see Timisjärvi *et al.*, 1982) for all calves weighed in the calving corrals in May and a daily growth rate of 302 grams for female and 315 grams for male calves weighed later during earmarking (Norberg *et al.*, 2005, 2006).

The daily survival estimates and 'reindeer days' (one 'reindeer day' = one radio collared reindeer out for one day) for the radio-collared calves were calculated using the Kaplan-Meier product/limit method (Kaplan & Meier, 1958) and using the computer program 'Kaplan-Meier survivorship analysis version 1.0' (Pol-

lock *et al.*, 1989) to obtain daily and total survival estimates for the study periods. Daily survival estimates were used to present survivorship curves between May/June and October. For calculating monthly survival estimates, cause-specific mortality rates and 95% confidence limits, the program 'Micromort version 1.3' (Heisey & Fuller, 1985) was used.

The survival estimates were calculated based on documented cases, i.e. only the calves that 1) were found dead, 2) had dropped their radio-collars during the study or 3) were recovered in the autumn/winter round-ups (survivors) when radio-collars were taken off were included in the survival analysis. The statistical differences in calf weights in different groups were tested using t-test and stepwise logistic regression. In addition to weight, also the effect of sex, pelt colour, study year and possible interactions on survival probability were investigated using logistic regression. Statistical tests were carried out by use of SPSS ver. 7.0 for Windows. The data were examined for statistical significance at $P < 0.05$.

Results

Of 806 reindeer calves radio-collared in Ivalo reindeer-herding cooperative during 1999-2001 in total 4.6% (37 calves) was found dead, 90.4% survived and 5.0% was not recaptured until the end of the study (annual monitoring from marking until the end of October). Of 919 radio-collared calves in Käsivarsi cooperative during 2002-04 in total 5.2% (48 calves) was found dead, 87.4% survived and

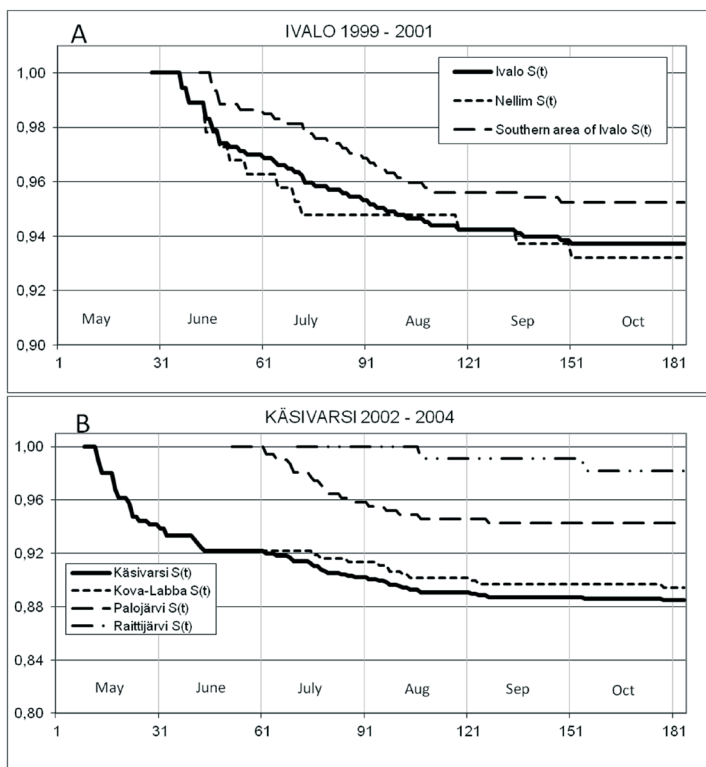


Fig. 2. Survivorship curves for radio-collared reindeer calves (A) in Ivalo cooperative and in its herding-groups during 1999-2001, and (B) in Käsivarsi and its herding-groups during 2002-2004. Day 1 is 1st of May. (Mortality (M) = 1 – Survival (S)).

7.4% was not recaptured, respectively. Highest area-specific annual mortality occurred in Ivalo in 2000, when in total 19 (51.4% of all dead calves) were found dead, and in Käsivarsi in 2004, when 20 radio-collared calves (41.7%) were found dead.

Pooled survival estimates in the cooperative of Ivalo (including all radio-collared calves during years 1999-2001) and in the cooperative of Käsivarsi (years 2002-04) were 0.937 (SE=0.011) and 0.885 (SE=0.011), respectively. Survival function curves (pooled data for the whole study) for the cooperatives of Ivalo and Käsivarsi as well as for the five different herding groups studied are presented in Figs. 2 A and B.

Table 1. Survival and cause-specific mortality estimates of radio-collared reindeer calves in the studied reindeer herding-cooperatives and herding-groups during study periods in 1999-2004. The survival and mortality estimates with 95% CI are calculated according to 2-week intervals using software Micromort 1.3. Number of death cases is in parenthesis.

District	Years	Radio days	Survival estimate	95% CI	Eagle (<i>n</i>)	Other pre-dation (<i>n</i>)	Other causes (<i>n</i>)	Unknown (<i>n</i>)
Ivalo	1999-2001	96 106	93.2	90.7-95.7	2.1 (16)	0.8 (4)	1.6 (7)	2,3 (10)
Nellim ¹	1999-2001	26 918	93.0	89.4-96.7	3.0 (6)	1.1 (2)	0.5 (1)	2,3 (4)
Ivalo south	1999-2001	69 188	92.6	87.9-97.6	1.7 (10)	0.3 (2)	4.3 (6)	1,1 (6)
Käsivarsi	2002-2004	107 885	88.0	83.5-92.7	3.0 (16)	0.6 (4)	4.0 (9)	4.3 (19)
Kova-Labba	2002-2004	58 492	89.0	84.3-93.8	3.1 (11)	0.5 (2)	3.7 (5)	3,6 (11)
Palojärvi	2002-2004	37 065	94.3	91.7-97.0	1.7 (5)	0.6 (2)	1.4 (4)	2,0 (6)
Raittijärvi	2002-2003	12 328	98.2	95.7-1.0	0.0 (0)	0.0 (0)	0.0 (0)	1.8 (2)

¹ in 2001 only 1400 radio days for Nellim herd (no dead calves were found)

The mortality estimate ($M=1-\text{Survival}$) of the calves radio-collared in Nellim area (cooperative of Ivalo) during calving time in May/June and monitored to end of October was 0.051 (SE=0.026) in 1999 and 0.086 (SE=0.038) in 2000. Pooled mortality for both study years in Nellim was 0.067 (SE=0.022). The annual mortality estimates of calves radio-collared in calving corrals in Kova-Labba herding-group (cooperative of Käsivarsi) in 2002-04 were 0.051 (SE=0.021), 0.093 (SE=0.027) and 0.118 (SE=0.042), respectively. Including also additional calves radio-collared in midsummer earmarkings in Kova-Labba, the annual mortality estimates were 0.049 (SE=0.018), 0.115 (SE=0.029) and 0.146 (SE=0.036) in 2002-04, respectively. The pooled three-year mortality in Kova-Labba was 0.090 (SE=0.017). In total 52% of mortality among calves radio-collared during calving in Nellim and 87% of mortality in Kova-Labba took place before the end of June.

The pooled mortality estimates of calves radio-collared during earmarking in June/July were 0.048 (SE=0.012) in Southern area of Ivalo (years 1999-2001), 0.018 (SE=0.013)

in Raittijärvi (years 2002-03) and 0.057 (SE=0.013) in Palojärvi (years 2002-04), respectively (Figs. 2A and B). Pooled mortality estimates for corresponding time periods (from 15 June until the end of October) were 0.047 (SE=0.018) in Nellim and 0.030 (SE=0.009) in Kova-Labba areas.

The annual mortality estimates analysed from midsummer earmarkings until the end of October in Southern area of Ivalo cooperative were 0.080 (SE=0.037), 0.085 (SE=0.027) and 0.016 (SE=0.010) for years 1999-2001, respectively. In Palojärvi, the southernmost herding-group of Käsivarsi, annual mortality estimates were 0.051 (SE=0.022), 0.056 (SE=0.024) and 0.074 (SE=0.024) for years 2002-04, respectively. Marking time of calves was latest in Raittijärvi, the northernmost herding-group of Käsivarsi, and took place mainly during the second week of July both in 2002 and 2003. In 2002 not any of the radio-collared calves were found dead in Raittijärvi area, and calves survived well also in 2003 mortality estimate being 0.034 (SE=0.24). For comparison with other herding-groups of Käsivarsi (time period July-October), the annual mortality estimates

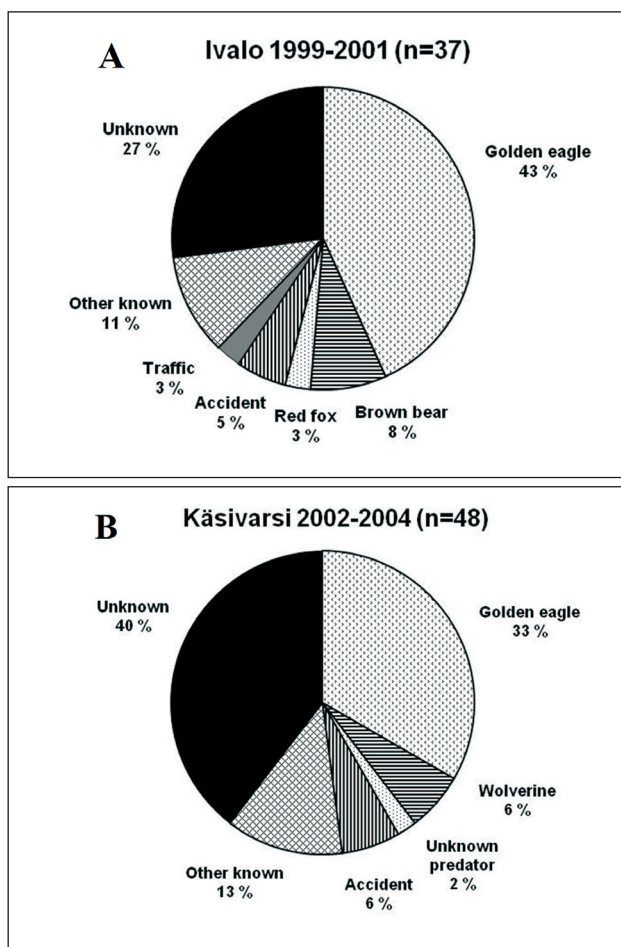


Fig. 3. The distribution of all death causes for radio-collared calves found dead (A) in Ivalo and (B) in Käsivarsi reindeer-herding cooperative during the study.

among all calves marked in Kova-Labba (both in the calving corrals and in midsummer ear-markings), were 0.007 (SE=0.007), 0.042 (SE=0.019) and 0.043 (SE=0.022) in 2002-04, respectively.

Golden eagle was the most significant cause of death in Ivalo and Käsivarsi cooperatives killing 0-3.5% of radio-collared calves in different study areas and years. Most calves killed by golden eagle (totally 11) were found in Kova-Labba herding-group in Käsivarsi during 2002-04. Five eagle-killed calves were found in Palojärvi herding group, while in Raittijärvi no calves killed by golden eagle were found.

In Ivalo cooperative golden eagle killed during 1999-2001 in total 16 calves, of which 6 were calves from Nellim herd. In pooled data including all radio-collared calves during the whole study, predation by golden eagle comprised on average 2% mortality rate in Ivalo and 3% mortality rate in Käsivarsi (Table 1). Golden eagle predation was observed already on calving grounds, but peaked in July-August, when reindeer preferred higher elevations for grazing and escaping insect harassment. Most calves (24 from 32) killed by golden eagle were found in the open areas, as in highlands, bogs and clear-cut forest areas. In Ivalo cooperative, 72 % of the golden eagle predation occurred in the forested habitats, including 22% of open clear-cut or seedling stands areas. In Käsivarsi cooperative, due to higher proportion of open mountainous landscape, 85% of golden eagle predation and 79% of other mortality occurred in fell habitats. The rest of eagle predation (15%) occurred on mires.

On average 54% of the radio-collared calves found dead in Ivalo and 42% in Käsivarsi cooperatives were attributed to predation, respectively. Golden eagle predation accounted for 33-43% of the cases and 80% of all identified predation (Figs. 3A and B). In Ivalo some calves were killed also by brown bear (8% of all calves found dead) and red fox (3%), and in Käsivarsi by wolverine (6%) and unidentified predator (2%). Mortality rates caused by other predators than golden eagle were on average less than one percent in both study cooperatives. Yet, bear-caused mortality was higher in Nellim than in the southern area of Ivalo (Table 1).

The share of other identified causes of death (accidents, traffic, others) was in both cooperatives 19%, while 27-40% of the succumbed

calves were associated with unknown causes of death. In Ivalo during 1999-2001 a total of 8% of all calves found dead, succumbed in accidents and in traffic, while 6% succumbed in accidents in Käsivarsi, respectively. Other causes (11-13%) included in both cooperatives disease, stress and poor condition of calves. When calves with unidentified cause of death were excluded from distribution, predation comprised on average 74% of the observed mortality (i.e. of calves with identified cause of death) in Ivalo and 69% in Käsivarsi.

The average adjusted (on June 1st, weighed in the calving corrals in May) weight of those radio-collared calves that survived in Ivalo cooperative was significantly higher (mean 9.8 kg, SD=2.0 kg, $n=169$) than weight of succumbed calves (mean 7.8 kg, SD=2.2 kg, $n=12$; $t=2.79$, $df=179$, $P=0.006$). According to the stepwise logistic regression, male calves had higher risk to die than female calves (Wald=9.88, $df=1$, $P=0.002$), and weight had significant effect for survival of male calves (Wald=8.30, $df=1$, $P=0.004$), but not on survival of female calves. Calves killed by golden eagles were significantly and 1 kg lighter (mean 7.2 kg, SD=2.2 kg, $n=5$; $t=2.47$, $df=172$) than calves that survived, and also lighter than those calves that succumbed due to other causes (mean 8.2 kg, SD=2.4 kg, $n=7$). Also in Kova-Labba herding group in Käsivarsi cooperative calves killed by golden eagles were 1.7 kg lighter (mean 10.7 kg, SD=1.4 kg, $n=5$) than those calves that survived (mean 12.4 kg, SD=1.9 kg, $n=259$; $t=1.9$, $df=262$, $P=0.053$).

The average adjusted (on July 1st, weighed in earmarking in June/July) weight of the radio-collared calves that were killed by golden eagles in the Ivalo cooperative was significantly lower (mean 12.8 kg, SD=1.7 kg, $n=11$) than the mean weight of survivors (16.6 kg, SD=2.5 kg, $n=560$; $t=760$, $df=10.84$, $P<0.001$). Likewise, the mean weight of calves killed by all predators was significantly lower (13.1 kg,

SD=1.7 kg, $n=13$) than the mean weight of the surviving calves ($t=7.05$, $df=13.17$, $P<0.001$). Similarly, the weight of the calves killed by golden eagles in the Palojärvi herding-group in Käsivarsi was significantly lower (mean 13.0 kg, SD=1.7 kg, $n=5$) than the mean weight of survivors (19.3 kg, SD=3.4 kg, $n=280$; $t=409$, $df=283$, $P<0.001$). Furthermore, the mean weight of the calves killed by all predators was significantly lower (12.2 kg, SD=2.2 kg, $n=7$) than the mean weight of the surviving calves ($t=5.46$, $df=285$, $P<0.001$). The weight of calves killed by golden eagles in Kova-Labba herding group was very low and significantly lower (mean 7.2 kg, SD=3.2 kg, $n=6$) than the mean weight of the surviving calves (13.4 kg, SD=4.3 kg, $n=28$; $t=3.03$, $df=31$, $P=0.005$). The weights of calves killed by golden eagles or other predators did not differ from the weights of calves that succumbed due to other causes in Ivalo nor in Käsivarsi. Moreover, no significant effect of pelt colour on calf survival was found in the present study.

Discussion

In most mammal species the mortality curve is typically U-shaped and the neonates and juveniles suffer the highest mortality, which then gradually decreases towards the prime-aged individuals (Caughley, 1966). Also in Svalbard wild reindeer (*Rangifer tarandus platyrhynchus* Vrolik), existing in an environment almost free of predators, mortality rates follow this U-shaped pattern, with higher mortality rate among calves and old animals than in middle aged individuals. Mortality rates in calves of Svalbard reindeer are calculated to 1% and 19% in the age intervals 0-6 and 6-12 months (Reimers, 1983). The mortality rates among 0-6 months-old reindeer calves is expected to be within the range of 6-21% found in the predator-free South-Georgia (Leader-Williams, 1980), and lower than 45-60% found in many *Rangifer* herds subjected to predation

(Reh binder, 1975; Bergerud, 1980). Wolves, bears and golden eagles have been the most important predators of radio-tagged reindeer/caribou calves in both North America and Russia, and in a study by Bergerud (1988) even 80-89% of deaths of caribou were caused by predation.

Many studies on reindeer/caribou have demonstrated that calf mortality is usually highest during the first days and weeks after calving and then decreases considerably during summer and autumn (see Eloranta & Nieminen, 1986; Whitten *et al.*, 1992; Adams *et al.*, 1995; Norberg *et al.*, 2005, 2006). It is important to note here that, the shape of the survivorship function curve is associated with the starting date of the study and composition of local predator guild, i.e. which species and in which numbers are found in the area of interest. For example, the study in the southern herd of Ivalo was started from the second week of June, while bear predation commonly peaks already at the turn of May and June (see Adams *et al.*, 1995; Young & McCabe, 1997). Thus, by being unable to mark calves already at calving may lead to underestimates of total calf mortality and leave some mortality-agents, such as bear predation, incompletely observed. Indeed, most bear predation in our study was observed in Nellim area, where calves were radio-collared in calving corrals.

Mortality estimates found in this study were significantly lower than the total mortality from August 1995 to April 1996 in North-Trøndelag in Norway (31%) (Nybakke *et al.*, 2002). The estimates were also lower than in the study conducted in the 1980s in Umbyn, Sweden, where mortality from July to April was 14%, and was mainly caused by lynx and wolverine (Björvall *et al.*, 1990). However, in the present study calves were radio-collared partly at the calving areas in May and radio-tracking was conducted until the early winter round-ups, when radio-collars were removed from the

survivors. Winter mortality, which may comprise substantial losses in *Rangifer* herds (e.g. Reimers, 1983), due to severity of the winter or presence of large carnivores, was not investigated in the present study. By comparing the results of Björvall *et al.* (1990) with the present study using corresponding period of follow-up, one notices, that the mortality estimate between July and October is similar or even lower in the Swedish study being 4-5%. The mortality estimates from the Swedish study fit within the annual variation in survival both in Ivalo and Käsivarsi. The closest reference for Ivalo and Käsivarsi, however, is from the earlier Finnish study by Norberg *et al.* (2006). The mortality estimate from July until the end of subsequent January was ca. 8.5% in both years, and 10.7% in pooled data comprising time period from calf earmarking in late June until the end of October.

The majority of semi-domesticated reindeer calves are born in northern Finland in May (peak calving taking place on 18-23 May: Eloranta & Nieminen, 1986; Weladji *et al.*, 2006), and in present study, totally 52% of calf mortality in Nellim and 87% in Kova-Labba reindeer-herding groups took place before the end of June. The annual mortality of the calves radio-collared during calving time in May and monitored to the end of October was maximally 11.8% (Kova-Labba in 2004) and of the calves radio-collared during earmarking in June/July 8.5% (southern area of Ivalo in 2000). When including calves born later and marked at the midsummer earmarking, the mortality in Kova-Labba increased to 14.6% due to the fact that many of the radio-collared calves at that specific moment and place were calves of young females and thus born later and lighter than average. These calves had a higher than average probability of succumbing due to predation and other causes. As hypothesized, the mortality in the present study was highest during the first month(s) after marking.

According to Linnell *et al.* (1995) predation generally comprise the major share of the total mortality of juvenile ungulates. In a study conducted in central Norway 89% of the total mortality in calves monitored between August and subsequent April was due to predation, and 60% of calves with identified cause of death were killed by lynx. Predation comprised even higher proportion, 94% of all identified mortality, when examined from August to mid-November (Nybakke *et al.*, 2002). Also in northern Norway predation accounted for 75% of the calf losses during summer and winter, and lynx was the main predator (55%) (Mathisen *et al.*, 2003). In Kainuu, southeastern reindeer-herding region of Finland, predation comprised 70% of all calves found dead and 87% of all identified mortality. Predation by wolf, bear, lynx and wolverine comprised 38.4%, 20.3%, 9.0% and 2.3% of all radio-collared calves found dead in the cooperative of Halla, respectively (Nieminen, 2009, 2010).

In a study conducted in northeastern Finnish Lapland a minimum of 53% of the total mortality was also attributed to predation, golden eagle comprising 45% of all calves found dead and 65% of all identified mortality. Mortality caused by golden eagle comprised annually 3–4% within the radio-collared cohort in 1997–98 (Norberg *et al.*, 2006). In earlier studies conducted in central Norway, Nybakke *et al.* (1999) found golden eagle predation to account for 1–2% among radio-collared calves, while Kvam *et al.* (1998) observed a total mortality of 8%, and calves killed by golden eagle comprised 40% of all calves found dead. In the present study golden eagle was the most significant cause of death both in Ivalo and Käsivarsi cooperatives causing up to 3.5% annual mortality rate among radio-collared calves. However, the annual variation in survival as well as eagle predation in this study was high. In Ivalo cooperative, eagle predation was 2.8% in 1999, 3.4% in 2000 and 0% in 2001. The

lack of eagle predation during the last study year in Ivalo may be explained by extremely favourable conditions for reindeer: easy previous winter with little snow and virtually no insect harassment during summer.

In Fennoscandia, the diet of golden eagles is based mainly on different grouse species and mountain hare, which together comprise 76% of the prey items collected from the eagle nests. In this material reindeer calves comprise the second most common mammalian prey for golden eagle after hare (see Sulkava *et al.*, 1999; Nyström *et al.*, 2006; Johnsen *et al.*, 2007). In a study by Sulkava & Rajala (1966) about 9% of the prey found from the nests of breeding golden eagles in the Finnish reindeer husbandry area was reindeer calves. However, information based on the prey remains at eagle nests is not sufficient to explain the predator-prey relationship between golden eagle and semi-domesticated reindeer calves as all radio-collared calves killed by golden eagle in this study were found from terrain, not at the eagle nests. Yet, it is unclear to what extent the calves were killed by adult territorial eagles or subadult floaters. Based on feathers collected from the kill-sites, Norberg *et al.* (2006) suggested that most of the eagle predation on reindeer calves in the cooperative of Lappi was associated with subadult eagles. Findings in the present study support this observation.

In the present study most reindeer calves killed by golden eagle were found in the open areas in both cooperatives. This finding is supported by mortality studies in central Norway (Nybakke *et al.*, 1999) and in northeastern Finnish Lapland (Norberg *et al.*, 2006), in which most of the eagle-killed calves were also discovered in open alpine terrain. Thus, earlier and also present studies suggest that access to alpine and subalpine highlands is associated with an increased risk of golden eagle predation on reindeer calves. Alpine landscapes, as well as open mires and clear-cut areas are

preferred by both golden eagle and reindeer during summers (see Norberg & Nieminen, 2008). Especially in midsummer, when insect harassment drives reindeer herds to find open windy areas and snow patches at higher elevations (see Hagemoen & Reimers, 2002), there is both temporal and spatial overlap in habitat selection of the golden eagle and reindeer. However, earlier studies in Finnish Lapland have shown that golden eagles may kill reindeer calves also in September and even in October, when calves weigh usually over 40 kg (Norberg *et al.*, 2006). Most of the golden eagle predation in the present study occurred during July and August. However, one calf (out of a total of 32 eagle-kills in this study) was killed by golden eagle also in September.

It is very common perception that animals preyed upon are either smaller or in poorer nutritional condition compared to survivors, and several studies (e.g. Haukioja & Salovaara, 1978; Eloranta & Nieminen, 1986; Tveraa *et al.*, 2003) have shown that the body weight of reindeer calves at calving and also during the first summer is associated with survival. Although golden eagles are capable of killing ungulates up to the size of an adult reindeer in certain conditions (Bergo, 1987), they usually kill smaller than average calves (Nybakk *et al.*, 1999; Norberg *et al.*, 2005, 2006). In the radio-collar study conducted in central Norway (Nybakk *et al.*, 1999), calves were marked during July and early August, and calves killed by golden eagles weighed on average 2.7–4.1 kg less than calves that survived. Also in the present study, the weights of calves (adjusted to 1st June and to 1st July) killed by golden eagle were 1–3.8 kg lower than weights of survived calves. The mean weight of calves killed by all predators was also lower than the mean weight of the calves that survived, but there was no significant difference in weights of predator-killed calves compared to calves that died on other causes.

We conclude that access to, and use of alpine highlands and other open areas affected the risk of reindeer calves to get killed due to golden eagle predation, and subsequently also the temporal survival distribution in study cooperatives. Based on our results, we emphasize the relative importance of golden eagle as a mortality factor in the northern part of the Finnish reindeer husbandry area, where the proportion of open alpine landscape is much higher than in the southern area.

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References

- Adams, L.G., Springer, F.J., & Dale, B.W. 1995. Caribou calf mortality in Denali National Park, Alaska. – *Journal of Wildlife Management* 59(3): 584–594.
- Ahti, T., Hämet-Ahti, L., & Jalas, J. 1968. Vegetation zones and their sections in northwestern Europe. – *Annales Botanica Fennica* 5: 169–211.
- Bergerud, A.T. 1980. A review of the population dynamics of caribou and wild reindeer in North America. – In: Reimers, E., Gaare, E. & Skjenneberg, S. (eds.): *Second international reindeer/ caribou symposium. Directoratet for vilt og ferskvannfisk*, Trondheim, Norway, pp. 556–581.
- Bergerud, A.T. 1988. Caribou, wolves and man. – *Tree* vol. 3, no.3, pp. 68–72.
- Bergo, G. 1987. Eagles as predators on livestock and deer. – *Fauna Norvegica Series C, Cinclus* 10: 95–102.

- Björvall, A., Franzén, R., Nordkvist, M., & Åhman, G. 1990. Renar och rovdjur. – *Naturvårdverket forlag*, Solna, Sweden, 296 pp. (In Swedish).
- Boertje, R.D. 1984. An energy model for adult female caribou of the Denali Herd, Alaska. – *J. Range Manage.* 38: 468-473.
- Carstensen Powell, M. & DelGiudice, G.D. 2005. Birth, morphologic and blood characteristics of free-ranging white-tailed deer neonates. – *Journal of Wildlife Diseases* 41: 171-183.
- Caughley, G. 1966. Mortality patterns in mammals. – *Ecology* 47(6): 906-918.
- Danell, A.C., Andren, H., Segerström, P., & Franzen, R. 2006. Space use by Eurasian lynx in relation to reindeer migration. – *Canadian Journal of Zoology* 84: 546-555.
- DelGiudice, G.D., Fieber, J., Riggs, M.R., Carstensen Powell, M., & Pan, W. 2006. Long-term age-specific survival analysis of female white-tailed deer. – *Journal of Wildlife Management* 70: 1556-1568.
- Eloranta, E. & Nieminen, M. 1986. Calving of the experimental reindeer herd in Kaamanen during 1970-85. – *Rangifer* Special Issue No. 1: 115-121.
- Hagemoen, R.I.M. & Reimers, E. 2002. Reindeer summer activity pattern in relation to weather and insect harassment. – *Journal of Animal Ecology* 71: 883-892.
- Haukioja, E. & Salovaara, R. 1978. Summer weight of reindeer (*Rangifer tarandus*) calves and its importance for their future survival. – *Reports from Kevo Subarctic Research Station* 14: 1-4.
- Heisey, D.M. & Fuller, T.K. 1985. Evaluation of survival and cause specific mortality rates using telemetry data. – *Journal of Wildlife Management* 49(3): 668-674.
- Johnsen, T.V., Systad, G.H., Jacobsen, K.O., Nygård, T., & Bustnes, J.O. 2007. The occurrence of reindeer calves in the diet of nesting Golden Eagles in Finnmark, northern Norway. – *Ornis Fennica* 84: 112-118.
- Kaplan, E.L. & Meier, P. 1958. Nonparametric estimation from incomplete observations. – *Journal of the American Statistical Association* 53: 457-481.
- Kojola, I. & Määttä, E. 2004. Suurpetojen lukumäärä lisääntyminen vuonna 2003. (The number and reproduction of large carnivores in 2003) – *Riistantutkimuksen tiedote* 194: 1-7. (In Finnish).
- Kvam, T., Kjelvik, O., Nybakk, K., & Overskaug, K. 1998. Effecten av simlas vinterbete og gjetin på vekt og overlevelse hos reinkalv. – In: Kvam, T. & Jonsson, B. (eds.). *Store rovdyns økologi i Norge. Sluttrapport, Norsk Institutt for Naturforskning*, pp. 168-172. (In Norwegian).
- Langenau, E.E. & Lerg, J.M. 1976. The effects of winter nutritional stress on maternal and neonatal behavior in penned white-tailed deer. – *Applied Animal Ethology* 2: 207-223.
- Leader-Williams, N. 1980. Population dynamics and mortality of reindeer introduced into South Georgia. – *Journal of Wildlife Management* 44: 640-657.
- Linnell, J.D.C., Aanes, R., & Andersen, R. 1995. Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates. – *Wildlife Biology* 1(4): 209-223.
- Mahoney, S.P., Abbott, L.H., Russell, H., & Porter, B.R. 1990. Woodland caribou calf mortality in insular Newfoundland. – In: Myrberget, S. (ed.). *Transactions of the XIXth congress of International Union of Game Biologists, Trondheim, Norway, Vol. I, Wildlife Management*, pp. 592-599.
- Maijala, V., Norberg, H., Kumpula, J., & Nieminen, M. 2002. Poron vasatuotto ja -kuolemat Suomen poronhoitoalueella. (Calf production and mortality in Finnish reindeer husbandry area) – *Kala- ja Riistaraportteja* nro 252, 62pp. (In Finnish).
- Mathisen, J.H., Landa, A., Andersen, R., & Fox, J.L. 2003. Sex-specific differences in reindeer calf behaviour and predation vulnerability. – *Behavioral Ecology* 14(1): 10-15.
- McCabe, T.R. 1997. Grizzly bear predation rates on caribou calves in northeastern Alaska. – *Journal of Wildlife Management* 61(4): 1056-1066.
- Miller, F.L. & Broughton, E. 1974. Calf mortality on the calving grounds of Kaminurik caribou, during 1970. – *Can. Wildl. Serv. Rep. Ser.* 26, 26pp.
- Nieminen, M. 2009. The impact of large carnivores on the mortality of semi-domesticated reindeer in Kainuu, southeastern reindeer-herding region of Finland. – In: *XXIX International Union of Game Biologists Congress, August 17-22, 2009, Moscow*, pp. 236-237.
- Nieminen, M. 2010. The impact of large carnivores on the mortality of semi-domesticated reindeer (*Rangifer tarandus tarandus* L.) calves in Kainuu, southeastern reindeer-herding region of Finland. – *Rangifer*, 30(1): 79-87.
- Norberg, H. & Nieminen, M. 2004. Vasakuolleisuus ja sen syyt Oivangin, Poikajärven ja Käsivarren paliskunnissa vuosina 2002-03. (Calf mortality and reasons in Oivanki, Poikajärvi and Käsivarsi co-operatives during 2002-2003). Report. 28pp. + 1 app. (In Finnish).
- Norberg, H. & Nieminen, M. 2008. Reindeer calves as prey for Golden Eagle in alpine and subalpine landscape: a spatio-temporal analysis. – In: K-O. Jacobsen (ed.). *Nordisk kongeornsymposium, Tromsø 25.-28. September 2008*. – NINA Rapport 442: 39-41.
- Norberg, H., Nieminen, M., Kumpula, J., Kojola, I., & Maijala, V. 2005. Poronvasojen kuolleisuus ja kuolinsyyt: yhteenveto telemetriatutkimuksista Suomen poronhoitoalueella 1997-2004 (Cause-specific mortality of radio-collared reindeer calves: a summary report of

- calf mortality studies in the Finnish reindeer herding area from 1997-2004). – *Kala- ja Riistaraportteja* nro 335, 65pp. (In Finnish).
- Norberg, H., Kojola, I., Aikio, P., & Nylund, M. 2006. Predation by golden eagle *Aquila chrysaetos* on semi-domesticated reindeer *Rangifer tarandus* calves in north-eastern Finnish Lapland. – *Wildlife Biology* 12(4): 423-432.
- Nybakk, K., Kjelvik, O., & Kvam, T. 1999. Golden eagle predation on semidomestic reindeer. – *Wildlife Society Bulletin* 27(4): 1038-1042.
- Nybakk, K., Kjelvik, O., Kvam, T., Overskaug, K., & Sunde, P. 2002. Mortality of semi-domestic reindeer *Rangifer tarandus* in central Norway. – *Wildlife Biology* 8(1): 63-68.
- Nyström, J., Ekenstedt, J., Angerbjörn, A., Thulin, L., Hellström, P., & Dalen, L. 2006. Golden eagles on the Swedish mountain tundra – diet and breeding success in relation to prey fluctuations. – *Ornis Fennica* 83: 145-152.
- Ollila, T. 2003. Viisi vuotta reviiriperusteista korvausjärjestelmää, tunnettujen reviirien määrää kasvanut. (Five years of territory based compensation scheme, the number of known territories has increased) – *Poromies* 70(1): 14-16. (In Finnish).
- Page, R.E. 1985. *Early caribou calf mortality in north-western British Columbia*. M.S. Thesis, Univ. Victoria, B.C., 143pp.
- Pollock, K.H., Winterstein, S.R., & Conroy, M.J. 1989. Estimation and analysis of survival distribution for radio tagged animals. – *Biometrics* 45: 99-109.
- Rehbinder, C. 1975. Kalvdödligheten i Ångeså samebys renhjörd. – *Nord. Vet. Med.* 27: 241-252.
- Reimers, E. 1983. Mortality in Svalbard reindeer. – *Holarctic Ecology* 6: 141-149.
- Sams, M.G., Lochmiller, L.R., Qualls, C.W., Leslie, D.M., & Payton, M.E. 1996. Physiological correlates of neonatal mortality in an overpopulation herd of white-tailed deer. – *Journal of Mammalogy* 77: 179-190.
- Skogland, T. 1991. What are effects of predators on large ungulate populations? – *Oikos* 61: 401-411.
- Sulkava, S. & Rajala, P. 1966. Kotkan pesimisaikaisesta ravinnosta poronhoitoalueella (Diet of the golden eagle (*Aquila chrysaetos*) during the nesting period in the Finnish reindeer husbandry area). – *Suomen Riista* 19: 7-19. (In Finnish).
- Sulkava, S., Huhtala, K., Rajala, P., & Tornberg, R. 1999. Changes in the diet of the Golden Eagle *Aquila chrysaetos* and small game populations in Finland. – *Ornis Fennica* 76(1): 1-16.
- Timisjärvi, J., Nieminen, M., Roine, K., Koskinen, M., & Laaksonen, H. 1982. Growth in the reindeer. – *Acta Vet. Scand.* 23: 603-618.
- Tveraa, T., Fauchald, P., Henaug, C., & Yoccoz, N.G. 2003. An examination of a compensatory relationship between food limitation and predation in semi-domestic reindeer. – *Oecologia* 137: 370-376.
- Valkenburg, P., McNay, M.E., & Dale, B.W. 2004. Calf mortality and population growth in the Delta caribou herd after wolf control. – *Wildlife Society Bulletin* 32(3): 746-756.
- Weladji, R.B., Gaillard, J.-M., Yoccoz, N.G., Holand, Ø., Myrsetrud, A., Loison, A., Nieminen, M., & Stenseth, N.Chr. 2006. Good reindeer mothers live longer and become better in raising offspring. – *Proc. R. Soc. B* 273: 1239-1244.
- Whitten, K.R., Garner, G.W., Mauer, F.J., & Harris, R.B. 1992. Productivity and early calf survival in the Porcupine Caribou Herd. – *Journal of Wildlife Management* 56: 201-212.
- Young, Jr., D.D. & McCabe, T.R. 1997. Grizzly bear predation rates on caribou calves in northeastern Alaska. – *Journal of Wildlife Management* 61(4): 1056-1066.

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Abstract in Finnish / Tiivistelmä: Vuosina 1999-2004 poronvasojen selviytymistä ja kuolleisuutta tutkittiin kahdessa paliskunnassa ja viidessä poronhoidon tokkakunnassa Pohjois-Suomessa. Yhteensä 1 725 vasalle laitettiin kaulaan venyvään pantaan kiinnitetyt kuolevuuslähettimet. Vasat punnittiin ja merkittiin 2-5 vuorokauden iässä vasontatarhoissa ja myös vasanmerkinnöissä kesä-heinäkuussa, jolloin vasojen ikä oli 2-8 viikkoa. Selvitettiin vasojen kuolemien suuruutta, ajoitumista ja syitä. Vuosina 1999-2001 löydettiin 4,6% radiopantavasoista kuolleen Ivalon ja 5,2% Käsivarren paliskunnassa. Radiopantavasojen keskimääräinen kuolleisuus vasonta-aikana toukokuussa ja seurattuna lokakuun loppuun asti oli 6,7% Ivalossa ja 9,0% Käsivarressa. Heinäkuusta alkaen keskimääräinen kuolleisuus vaihteli eri tokkakunnissa välillä 1,8-5,7%. Keskimäärin 54% kaikista kuolleenä löydetyistä radiopantavasoista Ivalossa ja 42% Käsivarressa oli petojen tappamia, ja maakotka oli merkittävin kuolinsyy molemmissa paliskunnissa tappaen 0-3,5% radiopantavasoista eri tutkimusalueilla ja -vuosina. Maakotkan osuus kaikista kuolleenä löydetyistä radiopantavasoista oli 33-43%, 55-59% selvitetystä kuolinsyistä ja 80% kaikesta selvitetystä petojen aiheuttamasta kuolleisuudesta. Useimmat kotkan tappamat vasat löydettiin heinä- ja elokuussa ja avoimesta maastosta, kuten ylängöiltä, soilta ja avohakkuualueilta. Radiopantavasojen paino toukokuussa (sovitettu painoon 1.6.) ja löydettyäessä kuolleenä kesällä oli merkitsevästi ($P<0,01$) alhaisempi kuin selviytyneillä vasoilla sekä Ivalossa että Käsivarressa. Edelleen keskikesällä kaikkien petojen ja myös maakotkan tappamien vasojen painot (sovitettu painoon 1.7.) olivat molemmissa paliskunnissa merkitsevästi ($P<0,001$) alhaisemmat kuin selviytyneiden vasojen painot. Petojen tappamien vasojen painot eivät kuitenkaan poikenneet muista syistä kuolleiden vasojen painoista. Tutkimuksen tulokset osoittavat maakotkan olevan suhteellisen merkittävä poronvasojen kuolleisuustekijä Suomen poronhoitoalueen pohjoisosassa.